

Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs

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ABSTRACT: Methods of assessing the structure and function of food webs are needed to provide a basis for assessing large-scale direct (e.g. fisheries) and indirect (e.g. climate change) effects of human activities on marine ecosystems. We present a simple synthesis of the complex structure and function of a real marine food web, based on analyses of body size distributions, production-body size relationships and trophic level-body size relationships. We show how size-based estimates of production, species richness and trophic level (from nitrogen stable isotope analysis) can be used to quantify trophic transfer efficiency, mean predator-prey body-mass ratios and the mean ratio of the number of predator to prey species in marine food webs. We applied these methods to the central North Sea, and estimated transfer efficiencies of 3.7 to 12.4%, a mean predator-prey body-mass ratio of 109:1 and a mean ratio of the number of predator to prey species of 0.34. We conducted sensitivity analyses to show how differences in the fractionation of $\delta^{15}\text{N}$ and changes in the slope of the relationship between production and $\delta^{15}\text{N}$ affected our predictions. Our estimates of transfer efficiency and mean predator-prey body-mass ratios are similar to those obtained by costly and labour-intensive diet- and ecosystem-modelling studies. Coupled analyses of size and trophic structure may provide a method for validating ecosystem models and assessing human impacts on marine ecosystems.

KEY WORDS: Body size · Food web · Transfer efficiency · Stable isotope analysis · Production · Diversity

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INTRODUCTION

The principle primary producers in marine ecosystems are small unicellular algae (Duarte & Cebrián 1996), and these support strongly size-structured food-chains where most predators are larger than their prey (Pope et al. 1994). Since many marine species will grow in mass by 5 or more orders of magnitude during their life cycle (Cushing 1975), and since cannibalism, cross-predation and transient predator-prey relationships are common (Pope et al. 1994, Boyle & Boletzký 1996), there are compelling reasons to adopt size rather than species-based analyses of marine food

webs (Sheldon et al. 1972, Kerr 1974). Body size determines potential predators and prey (Cohen et al. 1993), rates of production and natural increase (Banse & Moser 1980, Brey 1999), energy requirements (Boudreau et al. 1991) and vulnerability to mortality (Jennings et al. 1998).

Biomass size-spectra (plots of biomass as log body-mass class vs log body-mass class) have been used to describe the structure of aquatic ecosystems (Sheldon et al. 1972, Kerr 1974, Pope et al. 1988, Duplisa & Kerr 1995, Rice & Gislason 1996), and models of these size-spectra assume that biomass and production decrease in progressively heavier body-mass classes due to the inefficient transfer of carbon from prey to predators (Dickie et al. 1987, Thiebaut & Dickie 1992). This implies that heavier size-classes are higher in the

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trophic continuum, a pattern demonstrated empirically for plankton (Fry & Quinones 1994), benthic invertebrate (France et al. 1998) and fish (Jennings et al. 2002) communities. The trophic continua across body size-classes also show that fixed (integer) trophic levels do not appropriately describe the structure of aquatic food webs, and trophic level can thus refer to any point on the continuum.

Estimates of trophic transfer efficiency are needed to estimate unknown fluxes in production models, the potential yields of fisheries and the proportion of primary production required to sustain them (e.g. Pauly & Christensen 1995). Trophic transfer efficiency (TE) describes the proportion of prey production that is converted to predator production ($TE = P_c/P_p$, where P_c is predator production and P_p is prey production). Since body mass is correlated with specific production (Banse & Moser 1980), biomass size-spectra can be parameterised to give production by body-mass class (Platt & Denman 1978, Gaedke & Straile 1994, Duplisa & Kerr 1995). If mean predator-to-prey mass ratios can be estimated, then trophic transfer efficiency can be determined from the slope of the production size spectrum (e.g. Gaedke & Straile 1994). However, if trophic level at body mass is known, TE could be calculated without knowing the mean predator-prey body-mass ratio. This is because the slope of the relationship between trophic level and production at body size is the TE and the slope of the relationship between trophic level and body mass is the mean predator-prey body-mass ratio (as an output).

Trophic level can be estimated using nitrogen stable isotope analysis (Owens 1987), because the abundance of $\delta^{15}\text{N}$ in the tissues of predators is enriched relative to their prey (Minagawa & Wada 1984, Peterson & Fry 1987, Cabana & Rasmussen 1996, Post et al. 2000, Post 2002). Indeed, Fry & Quinones (1994), France et al. (1998) and Jennings et al. (2002) have already used nitrogen stable isotope analysis to show that the trophic levels of plankton, invertebrates and fishes in biomass size-spectra increase continuously with increasing body size. Nitrogen stable isotope analysis is preferable to diet analysis for estimating trophic levels in many marine food webs because most species switch their diet frequently, prey on species that are digested at different rates, have gut contents that cannot be identified, or regurgitate gut contents on capture (Staniland et al. 2001, Polunin & Pinnegar 2002). The abundance of $\delta^{15}\text{N}$ reflects the composition of the assimilated diet and integrates differences in assimilated diet over time (Minagawa & Wada 1984, Hobson & Welch 1992, Post 2002).

Broadly constant ratios of the number of predator to prey species may be a general property of parts of some food webs (Briand & Cohen 1984, Jeffries &

Lawton 1985). While such ratios cannot be determined accurately in food webs with taxonomic aggregation (Pimm 1982, Link 2002), ratios have been determined from species lists and knowledge of diet (Jeffries & Lawton 1985). In freshwater communities, these ratios range from 0.48 in species-poor collections to 0.29 in species-rich collections, with a mean of 0.36 (Jeffries & Lawton 1985). If relationships between body size, diversity and trophic structure can be described, then the slope of the relationship between trophic level and species richness at a given body size is the ratio of the mean number of predator to prey species.

In a previous paper, we used isotope analyses and size-spectra to describe trophic relationships within and among species and to describe the relationship between the size and trophic structure of a benthic fish and invertebrate community (Jennings et al. 2002). However, in this analysis, it was not possible to consider all pathways of energy flow through the food web, since some species of infauna and pelagic fish that interact with the benthic community, and contribute to production, were excluded. Here, we extend the population- and community-based approaches of Jennings et al. (2002) to the ecosystem, and quantify the abundance, diversity and $\delta^{15}\text{N}$ of all major groups of animals within a defined size range. We use these new data to integrate size-based production, diversity and stable isotope analyses and to establish relationships between production, diversity and trophic structure. We show that estimates of TE and predator-prey mass ratios derived from size-based analyses are comparable with those based on more data-intensive methods.

MATERIALS AND METHODS

We estimated the mean biomass and size distributions of all animals from 2 to 2048 g wet mass (excluding seabirds) in an area of the central North Sea from $54^{\circ}00'$ to $55^{\circ}00'$ N and $00^{\circ}30'$ to $02^{\circ}00'$ E. While animals of <2 g wet mass will account for most of the production in the marine ecosystem (e.g. Cushing 1975), we chose not to work with smaller animals for 2 reasons. First, the short-term (days, weeks) variability in the dynamics of plankton, meiofauna, small fishes and invertebrates means that they have to be sampled at intervals of a few weeks or less to produce meaningful time-averaged size-spectra (e.g. Pope et al. 1994). Second, the $\delta^{15}\text{N}$ of plankton and other small animals is highly variable and very frequent sampling is required to integrate this variability over the course of the production cycle (e.g. Rolff 2000). We did not have the resources (ship time) to sample very frequently and at large spatial scales and so we worked with larger ani-

mals (≥ 2 g in the case of the present study) that would integrate variability in the production dynamics and $\delta^{15}\text{N}$ of their smaller prey and would provide adequate time-averaged size and trophic spectra when sampled 2 times per year.

We used corers, dredges and nets to take haphazardly located replicate samples of infaunal invertebrates, epifaunal invertebrates, bottom-dwelling fishes and pelagic fishes or squid in autumn 2000 and spring 2001. The frequency of sampling with each gear, the methods of estimating abundance and the size ranges of animals sampled by each gear are described in Table 1. All individual animals in each replicate sample taken with each gear were weighed at sea and assigned to \log_2 size-classes. Weighing was done with calibrated Pols heave compensated balances with a resolution of 0.1 g and minimum accuracy of 0.2 g. We sorted infauna from the core/anchor dredge samples and invertebrate epifauna from the 2 m beam-trawl samples. Epifauna were defined as those species that live on the seabed or bury in it temporarily, while infauna were defined as those that live predominantly in the sediment.

We estimated the mean trophic level for the animals in each size-class using stable isotope analysis. Since each size-class of infauna and epifauna contained many animals of many species, comparable tissues could not be sampled, and all individuals that were

sampled with each gear in each size-class were homogenised in an electric blender. The size of the blenders used to homogenise the animals depended on the number of animals assigned to each size-class, and ranged from 0.25 to 2.5 l. Animals were homogenised whole, although shells were removed from infauna (Bivalvia) and hermit crabs (Paguridae). Approximately 4 g of homogenate was frozen at -30°C and retained for stable isotope analysis. For fishes in larger size classes (typically >32 g) we dissected a sample of white muscle from the dorsal musculature of each individual. Each fish was weighed before the sample was taken, and the sample size was set at a fixed percentage of body weight in each size-class, following the procedure described by Jennings et al. (2001b). The tissue from fishes in each size-class was combined and homogenised in a blender, or crushed and ground manually, to produce a smooth paste. Approximately 4 g of paste was retained and immediately frozen at -30°C .

The biomass and size-distribution of small pelagic fishes, predominantly sandeels, was estimated using acoustic methods (Table 1). For these fishes, we predicted trophic level from a relationship between trophic level and \log_2 body mass for sandeels caught with nets in the same area ($\delta^{15}\text{N}\text{‰} = [0.24 \log_2 \text{body mass}] + 11.4$). Biomass density by size-class for all animal groups was calculated as $B = (C/A) \times ac$, where B

Table 1. Equipment, methods and assumptions used to estimate the abundance of faunal groups. All sampling was conducted from the CEFAS research vessels 'Corystes' and 'Cirolana'. Sampling design: Years (seasons) \times Sites \times Replicates within sites, sites were 1 n mile² boxes for NIOZ core, anchor dredge and 2 m beam-trawl sampling; Area: area of replicate; Availability: proportion of total abundance of animals in group assumed to be in path of gear; Catch efficiency: proportion of animals in path of gear that are assumed to be caught. NIOZ: Netherlands Institute for Sea Research corer; GOV: Grande Ouverture Verticale otter trawl towed for 30 min at 4 knots (Knijn et al. 1993); na: not applicable

Group	Size-class	Gear	Sampling design	Area	Availability ^c / catch efficiency
Infauna	>2 g ^a	NIOZ core	$2 \times 12 \times 5$	0.1 m ²	1.0/ 1.0
Infauna	>2 g ^a	Anchor dredge	$2 \times 12 \times 3$	na ^b	na ^b
Epifauna	>2 g ^a	2 m beam trawl (2 mm mesh)	$2 \times 12 \times 3$	400 m ²	1.0/ 0.5
Small demersal fishes/squid	$>2-8$ g	2 m beam trawl (2 mm mesh)	$2 \times 12 \times 3$	400 m ²	1.0/ 0.5
Large demersal fishes/squid ^d	>8 g	4 m beam trawl (20 mm mesh)	$2 \times 12 \times 1$	14824 m ²	1.0/ 0.5
Large fishes/squid ^d	>4 g	GOV trawl (20 mm mesh)	$2 \times 3 \times 1$	variable ^e	0.5/ 0.5
Small pelagic fishes	>2 g	Acoustics ^e	na: grid survey ^f	2895 km ² grid ^f	1.0/ 1.0

^aShell free wet weights recorded for bivalve molluscs. The wet weights of bivalves (Bivalvia) and hermit crabs (Paguridae) exclude shells

^bAnchor dredge was used to obtain samples of infauna for stable isotope analysis, but not for abundance estimates

^cGeometry of net is not fixed

^dFish catches from the 4 m beam and GOV trawls were subsampled for stable isotope analysis

^eSurveyed with Simrad EK500 scientific echosounder operating at 38 and 120 KHz, calibrated according to standard methods (Foote et al. 1987). Post-processing of echosignals was performed using EchoView software (Sonardata). Biomass estimates were derived from 120 kHz echo integration data following MacLennan & Simmonds (1992) and MacLennan & Fernandes (2000). Target strengths were taken from unpublished tests and length-frequency data from pelagic trawl samples

^fNine north-south transects of 27 n miles spaced 6.75 n miles east-west were surveyed twice in both 2000 and 2001

Table 2. Biomass of sampled groups by \log_2 body-mass class. Mean (SD) biomass (g wet wt m^{-2})

Group	Body mass (midpoint \log_2)									
	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5
Infauna (NIOZ core) (excluding spatangoids)	1.62 (3.00)									
Epifauna (2 m beam trawl)	1.69 (0.24)	2.58 (0.25)	2.60 (0.33)	2.15 (0.41)	1.65 (0.38)	1.11 (0.34)	0.38 (0.14)			
Fishes (2 m beam trawl)	0.14 (0.04)	0.37 (0.10)								
Fishes (4 m beam trawl)		0.22 (0.03)	0.26 (0.07)	0.80 (0.15)	0.88 (0.19)	1.10 (0.22)	0.32 (0.08)	0.16 (0.04)	0.11 (0.04)	
Fishes (GOV trawl)		0.32 (0.28)	0.45 (0.28)	0.44 (0.25)	0.79 (0.22)	1.05 (0.40)	1.09 (0.53)	0.16 (0.07)	0.02 (0.02)	0.01 (0.01)
Fishes (acoustics)	1.73 (1.04)	2.90 (0.90)	1.73 (0.43)	0.52 (0.59)	0.01 (0.01)					

is biomass, C is catch, A is area swept or sampled by gear, a is the availability of the target group to the gear and c is the catchability of the target group in the path of gear (Table 1). The biomass of infauna was estimated from core samples (Table 1), but for infaunal stable isotope analysis we collected infauna at the same sites using an anchor dredge.

We calculated the total biomass of animals in each body-mass class as the sum of the biomass estimates from the different sampling gears. We assumed that the NIOZ (Netherlands Institute for Sea Research) corer/anchor dredge, beam trawls, GOV trawl (Grande Ouverture Verticale otter trawl) and acoustic survey all sampled different groups of animals, and summed biomass estimates for all these gears across size classes. This assumption is completely valid for the invertebrate infauna and epifauna that were sorted after sampling, but there will be a large overlap in the composition of demersal fish catches taken with the 2 and 4 m beam trawls. Accordingly, we only included fish of 2 to 8 g from the 2 m beam-trawl samples and fish > 8 g

from the 4 m beam-trawl samples (Table 1). There will also be a small overlap in the composition of demersal fish catches taken with the 4 m beam and GOV trawls, since both these gears will catch flatfishes and gadoids living on or near the seabed. However, studies of the catch efficiency of the GOV trawl for the closely bottom-associated flatfishes, that are caught most effectively with beam trawls, suggest that the extent of the overlap will be minor (e.g. Sparholt 1990).

Individual body mass was converted to production using a cross-species relationship between biomass and production (P) to biomass (B) ratios derived from the compilation of Brey (1999). The relationship was $\log_{10} P:B = -0.233 \log_{10} B - 0.197$, and the validity of the cross-species $P:B$ vs body-mass relationship has been verified using a phylogenetic comparative approach (Jennings et al. 2001a). For fish, $P:B$ ratios were taken as 4× those of invertebrates (Banse & Moser 1980). We excluded the production of burrowing urchins (spatangoids) from our analysis, even though they accounted for production of 9.6 $g\ m^{-2}\ yr^{-1}$. This is because the pro-

Table 3. $\delta^{15}N$ of sampled groups by \log_2 body-mass class. Mean (SD) $\delta^{15}N$ (‰)

Group	Body mass (midpoint \log_2)									
	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5
Infauna (NIOZ core) (excluding spatangoids)	8.00 (1.73)									
Epifauna (2 m beam trawl)	10.59 (0.80)	11.08 (0.74)	11.45 (0.71)	11.51 (0.60)	12.08 (1.41)	13.15 (1.59)	11.54 –			
Fish (2 m beam trawl)	10.92 (0.98)	11.75 (1.01)								
Fish (4 m beam trawl)		13.11 (0.51)	13.09 (0.28)	13.58 (0.42)	13.95 (0.57)	14.29 (0.56)	14.44 (0.60)	14.36 (1.29)	15.37 (0.78)	
Fish (GOV trawl)		12.30 (0.37)	12.45 (0.72)	12.49 (0.56)	12.79 (0.58)	13.35 (0.67)	13.50 (0.68)	13.46 (0.71)	15.00 (0.61)	15.37 –
Fish (acoustics)	11.76	12.00	12.24	12.48	12.72					

duction of these large deposit-feeders feeding at a low trophic level (mean $\delta^{15}\text{N} = 7.43 - 7.81\%$ in size-classes of 4 to 16 g) appeared to be decoupled from the rest of the food web we considered, and the production of burrowing urchins is largely recycled in the sediment by bacteria and meiofauna.

For stable isotope analysis, the frozen tissue from each target group and size-class was freeze-dried and ground to a fine powder (particles $< 60\ \mu\text{m}$). Samples of powder (1 mg) were weighed into a tin capsule, and the ^{15}N composition was determined using continuous-flow isotope ratio mass spectrometry (Preston & Owens 1983: PDZ-Europa Integra-CN system). Two samples of reference material (a standard mix of ammonium sulphate and beet sugar) were analysed after every 5 tissue samples to calibrate the system and compensate for drift. The ^{15}N composition was expressed in conventional delta notation, relative to the level of ^{15}N in atmospheric N_2 . Experimental precision was 0.1% (standard deviation of $\delta^{15}\text{N}$ for replicates of reference material).

Estimates of species richness in body-mass classes were based on all available records of infauna, epifauna and fish species that have been sampled in the study area since 1977. These records included ICES (International Council for the Exploration of the Seas) co-ordinated fish and benthos surveys (ICES unpubl. data, Heip et al. 1992, Knijn et al. 1993), the European Community-funded epibenthic survey of the North Sea (R. Callaway unpubl. data) and CEFAS (Centre for Environment, Fisheries and Aquaculture Science) research programmes (T. Dinmore & S. Jennings unpubl. data). We used a wide range of records over a long time period to ensure that estimates of maximum body mass were not primarily a function of the direct or indirect effects of fishing and to ensure that rare species were represented in our analysis. The absence of rare species in the samples we used for production and trophic level estimates will have little effect on these estimates because rare species account for a very small proportion of biomass and production. We assigned a maximum body mass (g) to all species and, with the exception of a few fishes that produce large egg cases or live young (elasmobranchs), we assumed that species would be present in their terminal (largest) body-mass class and all smaller classes. This is an appropriate assumption when predation is strongly size-based and cannibalism is common (Pope et al. 1994).

RESULTS

Biomass and $\delta^{15}\text{N}$ estimates for all size classes (Tables 2 & 3) enabled us to predict production and

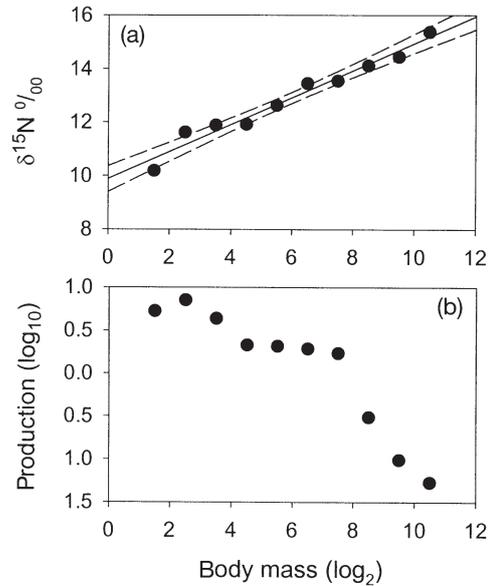


Fig. 1. Relationships between (a) biomass-weighted mean $\delta^{15}\text{N}$ (‰) and \log_2 body mass, and (b) \log_{10} production ($\text{g m}^{-2} \text{yr}^{-1}$) and \log_2 body mass for all faunal groups

weighted mean $\delta^{15}\text{N}$ across all animal groups. Total biomass and production by animals with a body mass of 2 to 2048 g were estimated as 29.3 and $25 \text{ g m}^{-2} \text{yr}^{-1}$ respectively, with $20 \text{ g m}^{-2} \text{yr}^{-1}$ of this production attributable to fishes. Biomass-weighted mean $\delta^{15}\text{N}$, calculated across all faunal groups, increased significantly with increasing body mass (Fig. 1a). If we assume that there is a 3.4% enrichment in $\delta^{15}\text{N}$ per trophic level (Minagawa & Wada 1984, Post 2002), then the relationship between trophic level and body mass ($\delta^{15}\text{N}\text{‰} = 9.88 + 0.50 \log_2 M$; $F_{1,8} = 227.6$, $r^2 = 0.97$, $p < 0.001$) implies that the mean predator-to-prey body-mass ratio in the community was 109:1 (mass ratio = $2^{3.4/\text{slope}}$).

The relationship between body mass and production suggested that production decreased increasingly fast with increasing mass in larger body-mass classes (Fig. 1b). The relationship between production and $\delta^{15}\text{N}$ by size-class was highly significant (Fig. 2a; $\log_{10} P = 5.48 - 0.420 \delta^{15}\text{N}$; $F_{1,8} = 29.6$, $r^2 = 0.79$, $p < 0.001$) and the slope suggests that the TE was 3.7% ($\text{TE} = 100 [10^{3.4 \times \text{slope}}]$). The relationship between species richness and $\delta^{15}\text{N}$ by size-class was highly significant (Fig. 2b; \log_{10} species richness = $3.81 - 0.138 \delta^{15}\text{N}$; $F_{1,8} = 120.1$, $r^2 = 0.94$, $p < 0.001$). The slope suggests that the mean ratio of the number of predator-to-prey species was 0.34 (ratio = $10^{3.4 \times \text{slope}}$).

Given that the high levels of fishing mortality observed in the North Sea are likely to reduce biomass and production in large body-mass classes, we tested

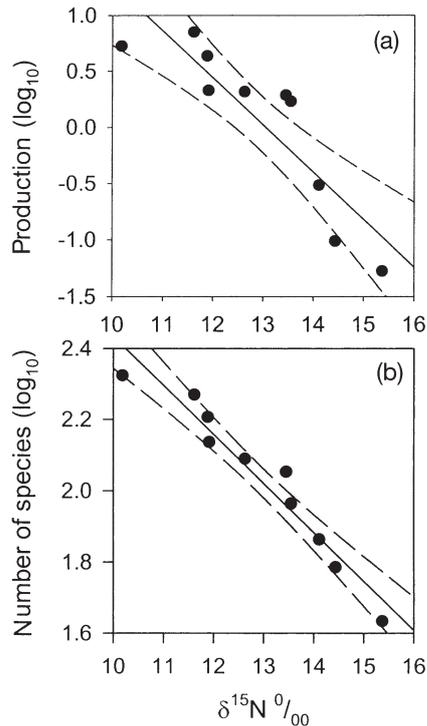


Fig. 2. Relationships between (a) \log_{10} production ($\text{g m}^{-2} \text{yr}^{-1}$) and weighted mean $\delta^{15}\text{N}$ (‰), and (b) \log_{10} species richness (number of species by \log_2 body-mass class) and weighted mean $\delta^{15}\text{N}$ (‰)

the relationship between production and $\delta^{15}\text{N}$ when the larger body-mass classes were excluded from the analyses (Fig. 3). When individuals with a body mass >1024 g were excluded, estimated transfer efficiency rose to 5.7%. When individuals with body masses >512 and >256 g were excluded, the estimated transfer efficiencies rose to 12.4 and 27.1% respectively (Fig. 3).

Since isotopic fractionation may not be 3.4‰, we calculated the effects of variations in fractionation on our estimates of TE (Fig. 4a), predator-prey body-mass ratios (Fig. 4a) and the mean ratio of the number of predator-to-prey species (Fig. 4b). Fig. 4 shows that a lack of knowledge or inaccurate assumptions about the degree of fractionation of $\delta^{15}\text{N}$ in the ecosystem would influence the outputs of our analyses.

DISCUSSION

Size-based analyses can be coupled with nitrogen stable isotope ($\delta^{15}\text{N}$) estimates of trophic level by body-mass class to estimate TE, mean predator-prey body-mass ratios and the mean ratio of the number of predator-to-prey species. We have shown that TE can be estimated without estimates of predator-to-prey body-

mass ratios, and our estimates of TE are comparable with those derived from ecosystem models (Christensen & Pauly 1993, Baumann 1995). Moreover, our approach gives mean predator-to-prey body-mass ratios as outputs, and these could be used to validate predator-to-prey body-mass ratios predicted from diet studies (Hahm & Langton 1984, Jennings et al. 2001b).

Analyses of the structure and function of ecosystems on large scales are inevitably ambitious, due to difficulties in sampling, identifying ecosystem boundaries, quantifying the import and export of production, and understanding the impacts of predators that are not included in the analyses (humans, seabirds, marine mammals; Steele 1974, Mann & Lazier 1986, Sherman & Alexander 1986, Bax 1991). Our approach relied on some largely untested assumptions about sampling efficiency, losses of biomass and production due to fishing, the extent to which predator-prey interactions in the study area are independent of those outside the area, and the fractionation of $\delta^{15}\text{N}$. Quantitative estimates of abundance depend on the efficiency of sampling gears, and efficiency is not well known for most of the species and size-classes that are caught in nets. As a result, we assumed constant catchability and availability for all size-classes. This could result in underestimates or overestimates of biomass and production for some size-classes, and thus bias our estimates of TE. Existing species-based models suffer from the same concerns about abundance estimation for diverse groups of animals that have to be sampled with different gears. The lack of good catchability and availability estimates for most sampling gears will continue to hamper ecosystem analyses.

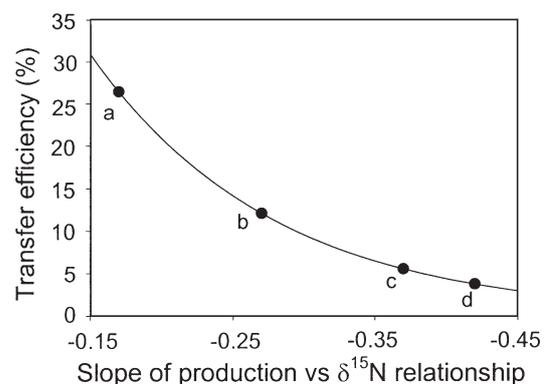


Fig. 3. Functional relationship between transfer efficiency and slope of the relationship between \log_{10} production ($\text{g m}^{-2} \text{yr}^{-1}$) and mean $\delta^{15}\text{N}$ (‰). Fractionation of $\delta^{15}\text{N}$ (‰) with trophic level is assumed to be 3.4‰. Circles a–d show how estimates of transfer efficiency change in relation to the size range of animals included in the analyses: a = 2–256 g included, b = 2–512 g included, c = 2–1024 g included, d = 2–2048 g included

Theorists suggest that TE may decrease at higher trophic levels and, by fitting a linear model to the production vs $\delta^{15}\text{N}$ relationship across all size classes, we have ignored this effect. However, the variance around our relationship, which we largely attribute to changing but unquantified catchability at body size and our relatively low levels of replication, meant that we could not reliably fit more complex models. Our approach may provide more accurate estimates of TE in areas that are less heavily fished and with smaller size-classes of animals that could be sampled more reliably. Reductions in biomass and, at high levels of mortality, production due to fishing will increase the slope of the production size-spectrum and reduce apparent TE. For this reason we repeated our analyses after excluding the production of larger fishes (Size-Classes 256 to 512 g, 512 to 1024 g and 1024 to 2048 g). The estimates of TE, when these classes were excluded, spanned the range recorded for many marine ecosystems (Baumann 1995). A useful development of the present approach would be to develop a size-based model of the effects of fishing on production, in order to create a theoretical production vs $\delta^{15}\text{N}$ relationship and a theoretical TE for an unfished community.

Another potential bias was the potentially inadequate sampling of larger pelagic species (predominantly herring and mackerel in body mass classes 128 to 512 g). These species feed at relatively low trophic levels and can be highly abundant in the study area. However, sampling may have been inadequate because they are seasonal visitors to the study area and their catchability and availability to trawl gears is lower than that of many demersal species. If the abundance of larger pelagic species was greater than our sampling suggests, then this would have increased the estimated predator-prey size ratio. Moreover, the inadequate sampling of larger pelagic species could contribute to the observed fall in total production with body size, and would mean that our estimates of transfer efficiency (calculated across body mass classes that include fish of 128 to 512 g) are too low.

The size-based approaches we have used assume that predator-prey relationships are principally determined by body size and that omnivory is widespread. There are good theoretical and empirical reasons to adopt size-based approaches (Kerr & Dickie 2001), but predator-prey relationships are constrained by many factors other than body size (Pimm et al. 1991, Hall & Raffaelli 1993), and our analyses are necessarily approximations of a more complex reality. While existing knowledge of the feeding habits of the larger fishes in the North Sea ecosystem is extensive and shows that the main pathways of energy transfer are size-based and that omnivory is widespread (e.g. Christensen 1995), some of the larger benthic infaunal species are

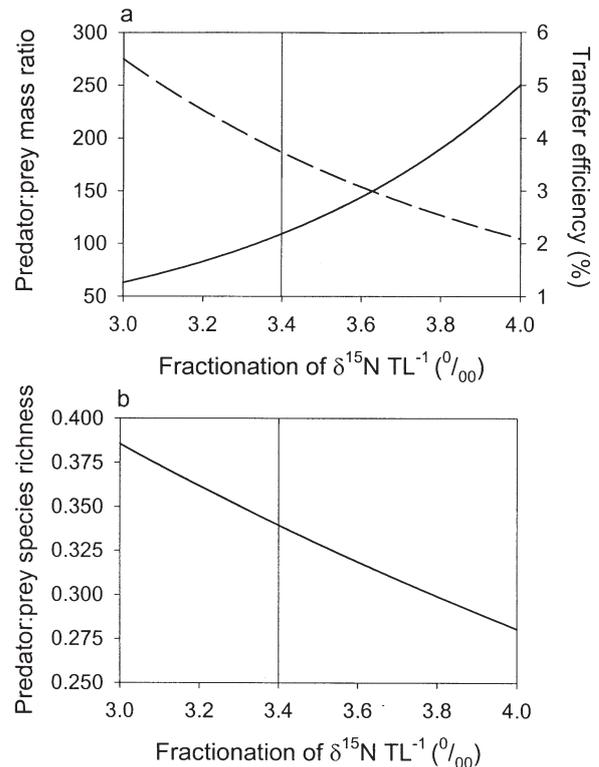


Fig. 4. Effects of assumptions about degree of fractionation of $\delta^{15}\text{N}$ (‰) with trophic level (TL) on (a) transfer efficiency (broken line) and predator-prey body-mass ratios (continuous line), and (b) mean ratio of the number of predator-to-prey species. Vertical lines in both graphs correspond to assumed fractionation of 3.4‰ per trophic level

unlikely to be components of size-based food webs. These larger benthic infauna include the spatangoid urchins that were excluded from this analysis, but could also include larger bivalves, such as *Arctica islandica*, which are only likely to be accessible to predators when damaged or exposed by trawling disturbance.

The biomass size-spectrum we compiled from the core, dredge, net and acoustic abundance estimates is effectively linear. Since we compiled the spectrum for animals that ranged in body mass over 3 orders of magnitude, we could be looking at part of a continuous spectrum or at part of a dome that corresponds to secondary scaling in the overall (from phytoplankton to large fishes) size spectrum (Sprules & Goyke 1994). Many aquatic size-spectra exhibit secondary scaling as biomass domes for phytoplankton, zooplankton and fishes, but the evidence for this has mostly been acquired from theoretical studies and studies in lakes (Kerr & Dickie 2001). In shallow marine environments such as the central North Sea, any secondary scaling in the spectrum may be less pronounced and the spectrum more continuous. This may be because lake

organisms can be classified into size groups that have a relatively limited range of life history traits and morphologies (Neill 1994), while our observations suggest that the range of morphologies and trophic levels of organisms in the central North Sea is wider. For example, the body-size ranges of the abundant benthic invertebrate fauna span the size range between large planktonic invertebrates and the small pelagic and demersal fishes. If biomass and trophic spectra are more continuous in the North Sea than in lakes, then the effects of predation on the food web will be more diffuse and apply across a wider range of trophic levels. This may explain differences in the significance of top-down control in regulating food web structure. In most lake ecosystems, there are strong and predictable effects of changes in predator abundance on the ecosystem (Carpenter et al. 1987), while these effects appear to be weaker and more transient in the many marine systems (Hallowed et al. 2000, Reid et al. 2000). Given that the presence and strength of secondary scaling in size-spectra will have a key impact on our interpretation of food web processes, further attempts to compile aggregate size-spectra for marine systems are needed. However, as we stressed previously, this will require much improvement in the quantitative sampling of epifauna and fishes.

We assumed that $\delta^{15}\text{N}$ was linearly related to trophic level, and a $\delta^{15}\text{N}$ enrichment of 3.4‰ per trophic level (Minagawa & Wada 1984, Post 2002). However, there is variation around the mean fractionation of 3.4‰, and this has prompted calls for further experimental validation (e.g. Gannes et al. 1997, Adams & Sterner 2000). Such validation has not been completed, and is probably not feasible, in a complex open-sea food web, although 9 mo experimental rearing of bass *Dicentrarchus labrax* fed on sandeel *Ammodytes marinus* and dab *Limanda limanda* diets at a range of ambient North Sea temperatures has shown that mean fractionation with both diets was 3.4‰ (C. Sweeting unpubl. data). The present experiments provide further support for the assumed fractionation, but are based on a situation where food was unlimited. We accept that food limitation, changes in dietary nitrogen content and changes in growth rate may influence fractionation (e.g. Adams & Sterner 2000), and we have shown how changes in fractionation would affect our results. To allow better interpretation of our results, and in order to assess the relative merits of TE predictions based on stable isotope data and estimates of predator-prey body-mass ratios, further experimental validation of $\delta^{15}\text{N}$ fractionation is required.

Our estimates of the mean ratio of the number of predator-to-prey species are not the direct equivalent of ratios that have been estimated in other systems (e.g. Jeffries & Lawton 1985), because not all the

species at one point on the trophic continuum will eat all smaller species. Thus, a number of invertebrate species are detritivores or herbivores and a proportion of planktivorous pelagic fishes (sandeel, sprat, herring) will not eat bottom-dwelling species once they have settled from the plankton. However, most larger fishes are generalists and would prey on most species 2 orders of magnitude smaller. Our estimate of the mean ratio of the number of predator-to-prey species (0.34) is similar to ratios reported for freshwater food webs (range 0.29 to 0.48, mean 0.36: Jeffries & Lawton 1985). Our methods for describing the ratio of the numbers of predator-to-prey species could readily be applied to other marine ecosystems, although they are only applicable across size ranges where species richness decreases consistently with increasing body size.

The relationship between $\delta^{15}\text{N}$ and \log_2 body mass is size-invariant and, if we assume that $\delta^{15}\text{N}$ fractionation is independent of body size, the relationship can be used to calculate mean predator-prey mass ratios. Our results show that the mean predator-prey mass ratio (109:1) is lower than that estimated for a community of bottom-dwelling fishes and epibenthos in the North Sea (434:1), but infauna and small pelagic fishes were not included in the community study (Jennings et al. 2002). Our study has shown that infauna and small pelagic fishes dominate the biomass of the smallest size-class, have low $\delta^{15}\text{N}$, and are consumed by many bottom-dwelling fishes and invertebrates. Predator-to-prey mass ratios are notoriously difficult to calculate from diet analysis (Ursin 1973, Hahm & Langton 1984), whereas predictions based on stable isotope analysis can account for animals feeding on complex and changing multispecies diets because they integrate changes in diet over time (Polunin & Pinnegar 2002). Our estimate of the mean predator-prey mass ratio falls within the range of $1:10^2$ to 10^3 that is assumed for many marine ecosystems (Cushing 1975).

Our size- and stable isotope-based methods of ecosystem analysis make a number of gross simplifications about the size-based nature of predator-prey relationships, the significance of omnivory in marine ecosystems, and the estimation of trophic level from nitrogen stable isotope analysis. However, they do provide a basis for assessing the structure and function of ecosystems at large spatial scales. We conclude that size-based analyses of the structure of a marine ecosystem can be coupled with nitrogen stable isotope estimates of trophic level by body mass to estimate TE, mean predator-prey body-mass ratios and the ratio of the number of predator-to-prey species, but that the results must be interpreted with caution and with reference to the underlying assumptions.

Encouragingly, our estimates of TE and mean predator-prey body-mass ratios are broadly consistent with

those obtained from costly and labour-intensive diet- and ecosystem-modelling studies. Coupled analyses of size and trophic structure may provide another method for validating ecosystem models and assessing human impacts on marine ecosystems.

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